

HOW THE BUTTERFLY LOST ITS SPOTS — A CLADISTIC EXCURSION

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We in England have a comfortably fixed idea of what a white butterfly should look like, and the green-veined white (Figs 1 and 4) conforms closely with this. Impoverished though the pattern is, in relation to pierid possibilities, its wings still provide a distinctive combination of radial and transverse melanic elements. How firmly established the genetic determination of its basic design is we can appreciate if we look at its close relatives in other lands — across Eurasia to Japan and on to California and Newfoundland. Minor variation certainly occurs: at high latitudes and altitudes the dark markings of the females may be extended, as if to compensate for low temperature by increased absorption of radiation. It does seem certain that here selection has acted, though its exact mode of operation remains controversial.

In North America there are many white subspecies which were formerly taken to belong to the same species, *Pieris napi* L. One of these, ssp. *oleracea* Harris, extends over much of the northern part of the United States and adjacent regions of Canada. But in its most characteristic form (Figs 2, 5 and 6) neither sex has any melanic marking on the upperside, beyond a few black scales on the veins at the forewing apex!

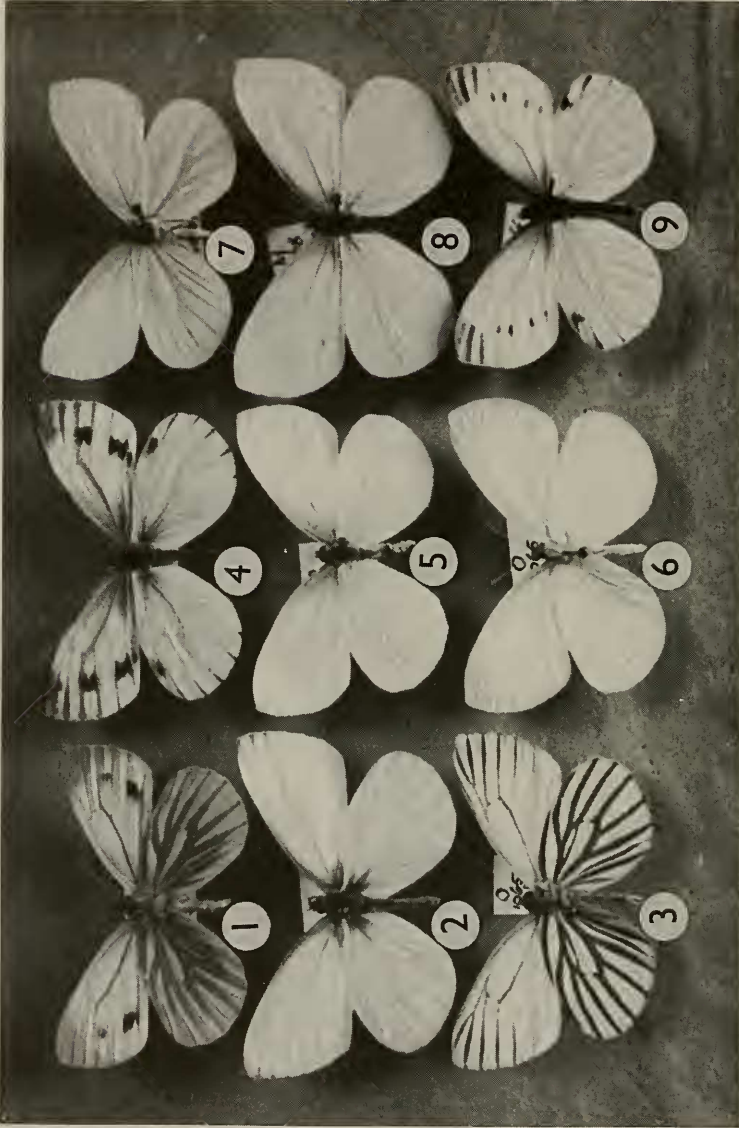
This insect has been much bred in captivity, and its F_1 and F_2 crosses with European *napi* are fertile. It is found that the reduction or loss of black markings is due to a recessive gene, 'restricta': thus the F_1 hybrid has markings of the European pattern, while in the F_2 about a quarter of the butterflies have reduced markings or none, the remaining individuals following *napi*.

If a hybrid female homozygous for *restricta* is examined, it is often found that some reduced marks do appear exactly in the place of the typical discal spots, but 'empty': that is, the dark scaling is confined to a border on the side of the vein as it passes a discal spot, and the spot's centre remains white (Fig. 9). Some specimens of pure *oleracea* offer exactly the same appearance, though in most of them the discal spots are mere traces or have disappeared completely.

One concludes that in some sense the typical *napi* pattern is still present in *oleracea*: that whatever singularities normally switch on production of melanin in certain cells have been unchanged in location.

The very similar (though specifically distinct) ssp. *virginiensis* Edwards, of rather more southerly distribution, also has severely reduced black marking. The results of crossing this with English *napi* suggest that here too the restriction is recessive, though the F_2 could not be obtained from this cross. *Virginiensis* can be hybridized with *oleracea*, but even the F_1 is far from vigorous: in this a few females even show slight radial markings, but in general black scaling is minimal, though again sufficient to show the survival of the under-pattern. The result is that expected from homozygous *restricta*, so it appears that these sometimes syntopic species carry similar *restricta* genes (this was confirmed experimentally in 1975).

In *oleracea* and *virginiensis* a typical development of *napi* markings is very unusual, and we think of *restricta* as fixed rather than polymorphic. Eitschberger (1983) figures an *oleracea* female from British Columbia with full marking, but this may be thought to be a translocated ssp. *pseudobryoniae* auct. Also, one supposes that where *oleracea* adjoins the well-marked *pseudobryoniae* or *venosa* Scudder, there must be some mutual introgression.



1 *napi* '86 ♀ viⁱⁱ 10 (underside). 2 *oleracea* '65 ♂ ♂ i'21 ('spring'). 3 *oleracea* '65 ♂ ♂ iⁱⁱⁱ 12 ('spring' underside). 4 *napi* '86 ♀ m 5. 5 *oleracea* '65 ♀ ♀ 30 ('summer'). 6 *oleracea* '65 ♀ ♀ 32 ('summer' underside). 7 *virginensis* '66 ♀ yⁱⁱ 11 (underside). 8 *marginalis* '68 ♀ ♂ iⁱⁱⁱ 8 ('summer'). 9 *napi* '86 ♀ h^{iv} 8.

In some other Nearctic subspecies, such as *Oregon marginalis* Scudder (Fig. 8), *restricta* seems to occur, but has not become fixed or is differently expressed. *Ssp. marginalis* has been crossed with *oleracea* and with several European stocks, but the genetics of its markings are insufficiently studied.

DISCUSSION

I think it is characteristic of the cladistic approach to classification to consider in the first place the alternative states of one character at a time, and on this basis to set up alternative dichotomous cladograms. Choice between these relies in the end upon the principle of parsimony, minimizing *ad hoc* assumptions, which seems to imply that the least unlikely thing does not fail to happen. If the cladistic technique can be applied at the specific-subspecific level, the green-veined white butterflies may be early victims. Let us see what might happen.

Restricta as wild type seems to be confined to North American whites: it never appears in Europe, nor in related Asiatic taxa such as *melete* Ménétrières and *dulcinea* Butler. Such a very limited geographic pattern of occurrence already suggests that *restricta* is the derived state. This is surely confirmed by the primitive *napi* marking's still having a ghostly existence in *restricta*.

How are we to regard the appearance of the same derived character in two nearly sympatric biological species? We should be unwilling to postulate identical genetic changes independently in two species adjacent to one another, by sheer coincidence.

Did *restricta* arise in one, then pass to the other while interbreeding was still not impossible? This would be really likely only if the character in question presented ecological advantages promoting positive selection. Such advantages would have to transcend difficulties of accommodating any trans-specific genetic reaction; if there were such major advantages, why has the character not spread more widely, in other adjacent populations?

The alternative possibility is that the genetic change took place before *oleracea* and *virginiensis* became separate. In that case *ssp. venosa* Scudder might represent the more primitive ('plesiomorphic') sister-group.

But another gene, the dominant 'acuta', producing (at least in the 'spring' generation) a rather narrow intensely melanic underside vein-marking, is shared by *oleracea* (Fig. 3) and *venosa* but not *virginiensis*. On the other hand, the diffuse underside marking of *virginiensis*, as well as that of the Alaskan *hulda* Edwards, is reminiscent of some European *napi*. *Oleracea*'s *acuta* form seems very bizarre to an English collector, but looks more commonplace among many east Asiatic species; it may therefore belong to the plesiomorphic alternative. *Virginiensis* may be the innovator also in another respect, if the bivoltine life-pattern is the primitive one in this group. Here again, the ghost of the bivoltinism remains in the ability of *virginiensis* to produce a summer generation in the laboratory.

But it would be rash to pursue this line of enquiry further without taking into consideration other genetically controlled characters which differ among the subspecies of the group, and without extending the scrutiny to the Palaearctic. Pupal and larval characters (if not hopelessly polygenic) can be employed too: this will probably involve maintenance of living stocks, but these will be desirable in any event, to explore the genetics and permit rejection of spurious identities. For example, how nearly is the 'subtalba' character of Nearctic *virginiensis* identical with that polymorphic in Palaearctic *bryoniae* Hübner? It would be well to find out. Nor should enzyme polymorphisms be neglected (Geiger & Scholl, 1985).

A character change must often take place through a temporary polymorphism. An apparently complete change concealing residual rare alternative morphs might

present some theoretical difficulties for phylogenetic practice. Wide sampling is a first essential, to reveal any polymorphism.

What sort of phylogeny may we expect to obtain? A nicely branching evolutionary family tree may reward our studies, but I suspect that it will not. We may find a character general in one species, but fixed in only part of another one. We can expect some parallelism, and if there has been hybridization of stocks there will be reticulation among the branches, or even unlikely-looking grafts. Nevertheless it will be surprising if we are able to confirm the real hybridity of many of Warren's supposed (1967) hybrid species, though it would be nice to think we might.

We may, of course, obtain a web of relationships incompletely compatible with present theoretical expectations. That would be even more interesting.

SUMMARY

Two Nearctic *Pieris (Artogetia)* subspecies have almost completely lost their characteristic upperside marking: one subspecies seems to have speciated since the loss. An exploration of relationships of the whole *napi/bryoniae/melete* group on the basis of (say) six to ten 'genetic' two-state characters is advocated: results may reveal the evolutionary route of the group's zoogeography.

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ANNOUNCEMENT

Nature Conservancy Council Invertebrate Survey of the New Forest. Society members who are not members of the New Forest Invertebrate Survey Team but who have post-1976 records of, or who make future visits to, the New Forest would assist the survey if they would send such records to the appropriate record-keeper as shown below.

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Diptera: Mr I. Perry, 27 Mill Rd, Lode, Cambridge CB5 9EN.

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Other orders: Mr S. R. Davey, HCMS Chilcombe House, Chilcombe Lane, Bar End, Winchester, Hants.